HOST-PARASITE RELATIONSHIPS OF ASCARIDOID NEMATODES AND THEIR VERTEBRATE HOSTS IN TIME AND SPACE

BY

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Osche (1958, 1963) presented the ascaridoids as an ancient group in excess of 200 million years old, steadily evolving in parallel with the vertebrates. He recognized that this progress was at times spasmodic or even explosive depending on the availability of host niches for exploitation, a concept further developed by Chabaud (1971) and Petter (1977). Based on Hartwich (1957), Osche formulated a phylogenetic system wherein primitive forms, represented by *Acanthocheilus* originating in selachians, progressed over evolutionary time as an ascending series of more highly evolved forms through fishes, amphibians, reptiles, birds and mammals. Superimposed on the parallel phylogenetic progression, he concluded that there have also been episodes of host-range-expansion (Wirtskreiserweiterung), whereby ascaridoids passed from one phylogenetic group to another and that this was especially achieved among piscivorous host groups.

HOST DISTRIBUTION

There have been several host lists compiled for ascaridoid nematodes (Stossich, 1896 ; Mozgovoy, 1953), but Osche may have been the first to draw attention to the relative distribution of ascaridoids among the vertebrate groups. He also analysed the ecological and behavioural features of their hosts, noted certain gaps in their host distribution, and pointed out those host groups in which ascaridoids have particularly flourished.

In considering the distribution of ascaridoids among their hosts, it is appropriate to divide them into two categories depending on the mode of nutrition of the host. Species in herbivorous hosts show evidence of physiological host-specificity because one particular species may be found to occur only in one or a few host species in a large host group. For example, *Parascaris equorum* occurs only in the genus *Equus* among the Perissodactyla and other animals grazing on the same pasture are seldom, if ever, found infected with this species. There are species in aquatic herbivorous hosts (e.g. sirenians) and in terrestrial herbivorous hosts (e.g. ox, hippopotamus, beaver, fruit bat, molerat, giant panda, and land tortoise). They are not a uniform group, but an assortment derived from various genera. Their restricted range suggests that herbivorous host groups have not usually provided a fertile field for dispersal. Most of the species probably have a direct life history pattern, infection occurring by ingestion of embryonated eggs, although contamination of food by minute intermediate hosts cannot be ruled out. With some species, such as *Toxocara vitulorum* in cattle and *T. pteropodis* in fruit bats, suckling animals are infected ; in the former, infection is via the mother's milk.

The second category, and this is the great majority of ascaridoids, comprises those which occur in hosts whose main source of food is another animal. Closely related genera such as *Terranova, Con-*

tracaecum, *Phocanema*, *Phocascaris*, *Anisakis* and *Galeiceps* occur in an assortment of fish, reptiles, birds, and mammals, whose common feature is their fish diet. This led Osche to formulate his hypothesis of host-range-expansion whereby, through ingestion of immature forms in common prey i.e. fish, adults were able to survive and mature in several different fish-eating host species, and thus widen their host range.

Another feature, related to their host-specificity and probably significant in their evolution, is the ability of some ascaridoid species to survive as adults in both prey and predator. For example, *Hexametra angusticaecoides* occurs in the adult stage both in chameleons and in their predators, the Madagascan boas. *Orneoascaris chrysanthemoides* occurs mainly in frogs, but also occurs in their predators e.g. the night adder. It seems probable that these are not spurious situations, but represent an adaptation whereby survival and continuance of egg-laying can occur in both prey and predator. This adaptation (host-succession-extension) may comprise another method, in addition to host-range-expansion, whereby ascaridoids have been transferred from one host group to a phylogenetically different group. This evolutionary " shortcut " from a prey group to a predator group was probably in some instances followed by suppression of the egg-laying stage in the prey host, so that the prey became an intermediate host. Further evidence that this might have occurred is that certain genera have species in prey-type hosts as well as in predator-type hosts, e.g. *Lagochilascaris turgida* in the opossum and *L. buckleyi* in the cougar, *Porrocaecum ratti* in rodents and *P. depressum* in raptorial birds, *Orneoascaris numidicum* in frogs and *O. varani* in monitors, *Toxocara mackerrasae* in rats and *T. cati* in felines. There are also pairs of genera whose structural similarity suggests that the genus in the predator is derived from the genus in the prey e.g. *Heterotyphlum* in fish and *Paraheterotyphlum* in sea snakes, *Orneoascaris* in frogs and *Ophidascaris* in snakes, *Terranova* in fish and *Phocanema* in seals.

The life history pattern of ascaridoids in exclusively carnivorous hosts probably always involves immature stages in tissues of animals which act as prey. These include vertebrates, especially fish, frogs, lizards, and small mammals, and also invertebrates, particularly earthworms, crustaceans, molluscs and insects. Ascaridoids occur as adults not only in dominant predators (sharks, pythons, crocodiles, eagles, tigers), but also in lowly predators (frogs, chameleons, blackbirds, rats). Infection of the definitive host occurs in both these categories through ingestion of immature stages living in the tissues of the prey. In this indirect or heteroxenous life history pattern one or more intermediate hosts are involved, the first intermediate host, usually an invertebrate, ingesting the eggs passed out in the faeces of the definitive host with sometimes a second intermediate host ingesting the first intermediate host. The parasite thus ascends a food pyramid whose complexity varies with the size and dominance of the definitive host, with a narrowing of host-specificity as the pyramid is ascended. These so-called life-pyramids can be marine, freshwater, or terrestrial depending on where the life history is enacted. They offer significant opportunities for both host-range-expansion and host-succession-extension, because the lower echelons of the pyramids in each ecological situation comprise a common pool of animals, arranged in several tiers, with invertebrates at the bottom, the lowly predators in the middle, and the dominant predators at the peaks. Speciation can thus occur across the peaks by host-range expansion and between the tiers by host-succession-extension. There are many variations on this pyramidal multi-tiered life history pattern and there can possibly be loss or addition of hosts at the bottom, in the middle, or at the top of the pyramid.

Distribution in Fishes. Two genera occur exclusively in elasmobranchs (*Acanthocheilus* in sharks and *Pseudanisakis* in rays), seven occur mostly in marine teleosts (*Thynnascaris*, *Raphidascaroides*, *Iheringascaris*, *Heterotyphlum*, *Lappetascaris*, *Aliascaris*, *Paranisakiopsis*). One occurs almost exclusively in freshwater fishes (*Raphidascaris*) and one occurs in both elasmobranchs and teleosts (*Paranisakis*). *Terranova* occurs in elasmobranchs, pigmy sperm whale, and crocodilians ; *Goezia* occurs in freshwater and marine teleosts, as well as in crocodiles and sea snakes. *Dujardinascaris* and *Brevimulticaecum*, usually in crocodilians, are occasionally collected from fish. It is difficult to be precise about how widespread all these genera are among fishes, because marine fishes of warm seas and freshwater fishes of the southern continents are inadequately surveyed. The genus *Thynnascaris* occurs in 30 or more families of marine teleosts and reputedly has undergone extensive speciation, whereas

Raphidascaris occupies a similar position in relation to the freshwater fish, occurring in 18 or more families, but has undergone speciation only at the extremities of its geographic range. *Paranisakiopsis* appears to be mainly restricted to the macrourid fishes. Other genera listed above are of indeterminate distribution.

Distribution in Amphibians and Reptiles. Among the Amphibians, ascaridoids have been found in none of the primitive forms and are represented by 3-4 species in the genus *Orneoascaris* occurring in only 6 of the 18 families of anurans, namely Ranidae, Bufonidae, Pipidae, Rhacophoridae, Pelobatidae and Brevicipitidae. Among reptiles they have a wide range, but there is marked variation in the different groups. They do not occur in *Sphenodon* and in lizards they occur only in three out of 18 families (*Orneoascaris* in Tejidae and Varanidae, *Hexametra* in Chameleontidae). In snakes they are better represented ; they are absent from the burrowing snakes, but occur in Hydrophiidae, Boidae, Colubridae, Viperidae, and Elapidae. *Ophidascaris* occurs in most of the terrestrial snakes, *Polydelphis* only in pythons. *Hexametra* occurs in Viperidae, Elapidae and Colubridae, *Travassosascaris* only in rattlesnakes. Depending on the species, infection is acquired through ingestion of frogs, lizards, or small mammals. The ascaridoids of anurans, terrestrial snakes, and lizards are closely related and probably have a common origin, whereas aquatic snakes harbour quite different genera, *Terranova* and *Contracaecum* in freshwater snakes, *Goezia* and *Paraheterotyphlum* in sea snakes. In chelonians there are three distinctly different and unrelated ascaridoids, *Angusticaecum* in land tortoises (the only adult ascaridoid in a herbivorous host outside the mammals), *Krefftascaris* in Australian freshwater turtles, and *Sulcascaris* in marine turtles. Crocodilians harbour a multiplicity of species and genera, about thirty distinct ascaridoid species arranged in eight or more genera being known to occur in these hosts ; most of them belong within the subfamily Heterocheilinae (*sensu* Sprent, 1980), but there are two species of *Terranova.*

Distribution in Birds. Ascaridoids of birds manifest a patchy distribution, many of the passerines and the galliforms, pigeons and parrots having escaped infection. There are two main groups, each comprising a distinct genus. *Porrocaecum* occurs in raptorial birds, such as hawks and owls, but also in several birds which feed on invertebrates (e.g. duck, thrush, starling, plover, crow, ibis, crane, etc.). *Contracaecum* occurs in fish-eating birds (gulls, cormorants, pelicans, herons, etc.).

Distribution in Mammals. Host distribution of adult ascaridoids in mammals has been recently discussed by Petter (1977) and she indicated that there are noteworthy gaps in their distribution. In most mammalian orders they are sparsely represented. They are not recorded in Prototheria (the record of *Ophidascaris radiosa* in *Echidna* by Schneider cited by Osche (1958) and Petter (1977) refers to a snake, *Bitis* [= *Echidna*], not an echidna). Among marsupials they are recorded in only 2 out of 8 families i.e. *Lagochilascaris* in Didelphidae in South America and *Baylisascaris* in Dasyuridae. In Insectivora the only recorded species is *Galeiceps cucullus* in the fish-eating *Potamogale.* In Edentata there is one species in Dasypodidae and in Chiroptera there is one species (*T. pteropodis*) in fruitbats. In Primates there are two species (*Ascaris petiti* in the " aye aye ", *Daubentonia,* in Madagascar, and *Ascaris lumbricoides* in man and apes). Ascaridoids are not known for certain in Pholidota, Lagomorpha, Tubulidentata, Dermoptera, or Proboscidea. Their occurrence in Artiodactyla consists of a few species scattered throughout the order, *Toxocara vitulorum* in *Bos*, *T. hippopotami* in *Hippopotamus*, *Ascaris suum* in *Sus*, *A. phacochoeri* in *Phacochoerus*, *A. mozgovoyi* in *Rangifer.* The Rodentia harbour several different ascaridoids but only in 5 out of 30 or more families ; *Baylisascaris* and *Ascaris* occur in the northern rodents (beaver, muskrat, molerat, squirrel and marmot), whereas *Porrocaecum* and *Toxocara* occur in South East Asian rodents. Some mammalian orders harbour unique genera, such as *Crossophorus* in Hyracoidea, *Heterocheilus* and *Paradujardinia* in Sirenia. As particularly stressed by Osche, fish-eating mammals in several orders tend to harbour closely-related ascaridoids. Cetacea harbour *Anisakis* and *Pseudoterranova*, Pinnipedia harbour *Contracaecum*, *Phocanema* and *Phocascaris*, otters and a fish-eating insectivore harbour *Galeiceps.* As was stressed by Osche (1958) and Petter (1977), it is only in the Carnivora that there is evidence of extensive radiation of ascaridoids in mammals. Many fissipede genera harbour one or more characteristic, but closely related ascaridoid species, for example *Baylisascaris transfuga* in *Ursus* and other bears, *B. procyonis* in *Procyon*, *B. schroederi* in *Ailuropoda*, *B. columnaris* in *Mephitis*, *B. devosi* in *Martes*, *Toxocara cati* in Felidae, *T. canis* in Canidae, *T. suricattae* in Viverridae. There are also several other species occurring in particular fissipedes with a limited range in particular locations, e.g. *T. melis* in badger, *T. vajrasthirae* in the hogbadger, *T. tanuki* in the raccoon dog, *T. alienata* in the coati and *Toxascaris versterae* in hyenas. It seems likely that infection is mainly spread through ingestion of rodents or other prey.

In summary, host distribution of ascaridoids is widespread, involving all the main vertebrate groups, but within these groups there is considerable variation in host distribution. Apart from the crocodilians, in which they have been reported in almost all the known species, and the fishes, in which the full extent of their radiation is not known, ascaridoids are of patchy incidence within the vertebrate classes. Distribution is not indicative of a gradual adaptive radiation throughout the vertebrates, but rather of a series of random, haphazard excursions. Successful exploitation appears to have depended on feeding habits and behaviour of the host group. Although there have been a few instances of successful exploitation of herbivorous hosts, these are mostly in mammals and have resulted in narrow host-specific host-parasite relationships with little or no radiation in the host group. Most success bas been achieved with carnivorous hosts, especially with the fish-eaters, the frog-eaters and the rodent eaters. They occur most consistently in predators such as sharks and rays, freshwater and marine teleosts, crocodilians, snakes, raptorial and fish-eating birds, toothed whales and Carnivora.

GEOGRAPHICAL DISTRIBUTION

In discussing geographical distribution, it is appropriate to divide the group into two ecological subgroups, the first comprising genera in hosts more or less unrestricted, the second comprising genera in hosts whose distribution is now restricted by geographical barriers, i.e. freshwater and terrestrial hosts.

The first group of genera are mostly in marine hosts and, as far as present knowledge indicates, many marine species extend throughout the range of their hosts. Nevertheless some speciation has occurred in marine hosts, especially in hosts which have for some reason become isolated ecologically or separated geographically. For example, the freshwater dolphin *Inia geoffrensis* of the Amazon has a distinctly different species of *Anisakis* from the species in its marine relatives. The Caribbean and Amazonian manatee have a different species of *Heterocheilus* from the Senegal manatee. According to Davey (1971) *Anisakis typica* is found in whales in warm water, whereas *A. simplex* occurs mostly in cold water. More data is required on the geographical distribution and speciation of genera occurring in elasmobranchs (*Terranova*, *Paranisakis*, *Acanthocheilus*, *Pseudanisakis*) and in teleost fishes (*Paranisakiopsis*, *Thynnascaris* and related genera). It seems possible but is certainly not proved that these genera occur wherever their particular host groups occur. Similarly *Paraheterotyphlum* and *Sulcascaris* probably occur wherever sea snakes and sea turtles occur, *Contracaecum* in cormorants, pelicans and fish-eating sea birds, *Paradujardinia* in dugongs, *Heterocheilus* in manatee, *Contracaecum* and *Phocanema* in seals, and so on. Although records are scanty for some regions, *Porrocaecum* in birds of prey and *Contracaecum* in fish-eating birds can probably also be placed in this unrestricted category because of the mobility of their hosts. Ascaridoids of domestic animals and man also have a potentially world-wide distribution.

Ascaridoids of terrestrial and freshwater hosts tend to show a discontinuous geographical distribution. An exception is *Goezia* whose species not only occur in a wider range of hosts, but have been reported in a wider range of ecological situations and over a wider geographical range than any other genus. There are a few genera whose species extend almost to the full range of their host groups, e.g. *Ophidascaris* in snakes, *Dujardinascaris* and *Terranova* in crocodilians, but most genera fall into categories based on their restricted distribution pattern as follows :

1) *Holarctic pattern.* Extensive east-west, but less extensive north-south dispersal. This pattern occurs with *Raphidascaris* in freshwater fishes and several genera (*Toxascaris*, *Toxocara*, *Bay-*

lisascaris) in placental carnivores. There is some spread into Africa, but little into South America and Australia.

2) *Old World Tropical pattern.* Main distribution in land masses (excluding Madagascar) bordering the Indian Ocean. This pattern occurs with *Ophidascaris* and *Polydelphis* in pythons, *Multicaecum* and *Gedoelstascaris* in crocodiles, *Orneoascaris* in monitors, frogs and toads, and to a more limited extent with *Toxocara* in rodents and fruitbats.

3) *South Atlantic pattern.* Main distribution in South America and Africa, with extension of some genera into Eurasia or North America. This pattern occurs with *Angusticaecum* in tortoises, *Brevimulticaecum* and *Ortleppascaris* in crocodilians and *Lagochilascaris* and *Galeiceps* in Carnivora.

4) *New World pattern.* Exclusive to Americas with variable north-south dispersal. There are surprisingly few ascaridoid genera recorded in freshwater fish in the southern parts of this region; they mostly belong to genera containing other species in reptiles (*Goezia, Brevimulticaecum*, and *Terranova*); there are no species recorded in amphibians. Indigenous genera in reptiles include *Travassosascaris* in crotaline snakes, *Brevimulticaecum* in caiman and alligator and " *Orneoascaris* " *alatum* in the tejid lizard *Tupinambis.* Whereas pythons have been shown to be infected with seven different *Ophidascaris* spp. the boas of South America (as well as those from Madagascar and New Guinea) have not been found to carry *Ophidascaris.* In snakes, *Hexametra, Travassosascaris* and *Ophidascaris* are well-established genera in South American colubrid and/or viperid snakes and their species bear a close resemblance, if they are not identical, to species in North American snakes. *Travassosascaris* is found only in America, whereas *Hexametra* extends to Africa and Asia. Excluding those species occurring in man and domestic animals, all of which seem likely to have arrived with European man, there are few indigenous ascaridoid species occurring in South American mammals. They include " *Ascaris* " *dasypodina* in Dasypodidae, *Toxocara alienata* in Procyonidae, *Lagochilascaris turgida* in Didelphidae, and *Galeiceps longispiculum* in otters. The closest relatives of the last three of these species are in Africa. Several ascaridoid species, well-established in North American mammals, appear to be rare or absent in related mammals of South America. This is unexpected in view of the probability that many mammals moved southwards when a land bridge became established. *Crocodylus acutus* in Central America barbours two species (*Dujardinascaris helicina* and *Terranova crocodili*) which are less closely related to those reported from the alligator and caimans than to those occurring in African crocodiles.

5) *Indo-Australian pattern.* Freshwater fishes in Australia are mostly secondarily adapted to freshwater; some of these carry *Goezia.* The only ascaridoid known in a primarily freshwater fish is a species found in an osteoglossid fish (*Scleropages*) and is related to species in crocodiles. There are no published records of species in anurans further east than New Guinea. Crocodiles harbour species in genera common to Africa (*Dujardinascaris, Gedoelstascaris, Terranova, Multicaecum*). The only genus (*Krefftascaris*) indigenous to the Region contains a single species in freshwater turtles. Genera in pythons, elapid snakes and varanid lizards (*Ophidascaris* and *Orneoascaris*) contain species which are distinct, but closely related to species in related hosts in Asia and Africa. *Hexametra* has not been recorded in Australian snakes. Australian marsupials, except for Dasyuridae, appear to have escaped infection. The species in dasyurids is a puzzle because its nearest relative occurs in Holarctic Mustelidae. There is insufficient evidence to indicate whether the dingo or the Australian Aborigine harboured ascaridoids before the advent of European man. Apart from man and domestic mammals, two groups of placental migrants to Australia harbour ascaridoids; these are *Toxocara mackerraeae* in rodents and *T. pteropodis* in fruit bats. The distribution of ascaridoid species in rats (*Porrocaecum ratti* and *Toxocara* spp.) appears to be restricted to India, South-East Asia and Northern Australia. *P. ratti* occurs in India and Thailand whereas *T. mackerrasae* occurs in Queensland and Thailand; *T. apodemi* occurs in Korea. Distribution in bats is even more restricted; fruit bats are infected in New Caledonia and Queensland, but further data is needed on the extent of distribution of *T. pteropodis* throughout the range of fruit bats; this species appears to be the only naturally occurring ascaridoid in Oceania; there are none in New Zealand.

6) *Equatorial pattern.* Distribution of ascaridoids in snakes (other than Boidae) and Croco-

dilians, extends more or less uniformly throughout the whole of their hosts' range which is now mainly in the equatorial regions. This applies to the genera *Terranova* and *Dujardinascaris* in crocodilians and to *Ophidascaris* in snakes (other than boas).

7) *Madagascar pattern.* Like other islands (Japan, Philippines, New Zealand), Madagascar has a paucity of ascaridoid species. None have been described in freshwater fish and although species in these genera are present in Africa, *Orneoascaris* has not been found in anurans, *Angusticaecum* in tortoises, or *Toxocara* in viverrids. Moreover, in spite of their widespread occurrence in pythons in Africa and India, *Ophidascaris* and *Polydelphis* have not been reported from the Malagasy boas. On the other hand crocodiles have a species of *Dujardinascaris*. chameleons have a species of *Hexametra*, and colubrine snakes have a species of *Ophidascaris*, each closely resembling or identical with African species. There is one endemic species, *Ascaris petiti* in a lemur.

In summary, the geographical distribution of Ascaridoidea is overwhelmingly concentrated in the Holarctic, Oriental and Ethiopian Regions. All the ascaridoid genera are represented in these regions, except for one in the Neotropical and one in the Australian Region. There is no indication of Gondwana distribution ; with few exceptions, the ascaridoid fauna of the Australian Region appears to have been carried by migrants from South-East Asia. Whereas species in crocodilians and snakes of South America are mainly close to North American forms, affinity of species in South American mammals and tortoises is mainly with African species. Ascaridoids of freshwater fishes in both South America and Australia appear to be more closely related to those occurring in crocodilians than to those in freshwater fishes in more northerly parts of the world.

COMMENT

The present writer tends to agree with Hartwich (1957) that the time is not ripe for speculation on the phylogeny of ascaridoids, because, lacking fossil evidence, our knowledge of host and geographical distribution is not sufficiently comprehensive or precise.

Being virtually absent from the most primitive members of each vertebrate class, from most burrowing and arboreal forms, and being relatively rare in herbivorous animals, the evidence does not support Osche's concept that ascaridoids are endowed with the adaptive ability to progress by parallel evolution throughout the vertebrates. Indeed it is abundantly evident that their host distribution has been determined for the most part by ethological and ecological rather than phylogenetic factors. On the other hand, without prejudice to the question of their actual origin, it seems reasonable to agree with Osche that the ascaridoids originated in aquatic animals and progressed from aquatic to terrestrial hosts. Having agreed to this, one is faced with selection of the aquatic vertebrate group most likely to have been their original hosts. Osche selected the selachians, but morphological considerations apart, distribution does not support this. Although they occur in several selachian families, the four ascaridoid genera involved are not a uniform group and the extent of their speciation is quite meagre. Freshwater fishes are an even less convincing choise, because the predominately northerly incidence of infection and the low extent of speciation in the single genus mainly involved (*Raphidascaris*) indicates a relatively recent invasion, probably after the freshwater fishes of the southern continents became separated. Marine teleost are a more likely selection because there is good evidence for widespread dispersal, with several genera and many species in these hosts, but we do not yet known the extent of their incidence in this host group. The anurans are unlikely as ancestral hosts because of their relatively late appearance and because of the very limited incidence of ascaridoids throughout the group as a whole. The chelonians too, with their three disparate ascaridoid genera, seem unlikely candidates. On the whole, it seems that the best case can be made for the Crocodilia, the grounds being that their ascaridoids are of relatively small size (a primitive feature according to Osche) and distributed throughout the whole geographic range of the host group. There are almost as many genera of ascaridoids in crocodilians as there are in the host group and they are of uniform structure. Even if the Crocodilia was not the original host group, this multiplicity of genera and species indicates that extensive dispersal occurred in this group.

Accordingly, the present writer would modify the proposals of Osche and, incorporating some of the concepts of Chabaud (1971) and Inglis (1965), present the following, admittedly speculative, concept of the evolution of ascaridoids. As mentioned above, the crocodilians are regarded as the most likely host group to have brought the ascaridoids to the Tertiary epoch; possibly they were forms similar to the present Heterocheilinae (*sensu* Sprent, 1980) and throughout the Tertiary these forms may have given rise to the forms in amphibians and terrestrial reptiles, birds and mammals. Moreover it seems likely that the centre for this radiation was the Old World Tropics, especially the deltas and estuaries of the great rivers. It is possible that there was already emerging another ascaridoid line in marine fishes, contemporary with the line in Crocodilia, and that these forms gave rise to the forms in freshwater fishes, and marine reptiles, birds and mammals. A diphyletic origin cannot be ruled out.

At first there was possibly a basic life history pattern involving a definitive host (crocodile) and an invertebrate (crustacean). However, with the ever-widening array of potential hosts, those animals which shared the crocodiles' diet were probably exploited as new definitive hosts through host-range-expansion. Aquatic life history pyramids would have been emerging, especially involving estuarine, freshwater and marine fish, whereby more dominant predator fish, marine reptiles, birds and mammals, were reached through host-succession-extension. It was the arrival of frogs, and later rodents, which were likely to have provided particular scope for establishment of terrestrial life history pyramids, whereby with ever-increasing opportunities for predation, monitors and snakes, raptorial birds, and mammalian carnivores could be reached by host-succession-extension, and new phases of radiation opened up.

Geographical distribution patterns indicate that during the main radiation of the ascaridoids, the disposition of the continents was much as it is today. Considerable migrations of host animals were afoot in the Tertiary and in some instances ascaridoids were no doubt carried with them, for example by snakes to Australia and South America, by carnivorous mammals to the northern regions. But in other instances, where definitive hosts were lowly predators like frogs and rats, ascaridoids were evidently lost in transit and defaunation resulted; so that these animals now act as definitive hosts for ascaridoids only where they originated i.e. in parts of the Old World Tropics. In other parts of the world, frogs and rodents now play the role of intermediate hosts, although a few herbivorous rodents have become secondarily infected, especially in the Holarctic Region.

Defaunation appears to have occurred especially in relation to island fauna, but discontinuous distribution had probably also resulted from extinction of hosts in part of a parasite's range, for example the discontinuous distribution of *Angusticaecum holopterum* was probably caused by extinction of its testudinid host in North America.

The evidence based on distribution indicates that, although they may have evolved in parallel with some host groups, the mainstream of ascaridoid evolution has been effected through (a) establishment of life history pyramids in marine, freshwater, and terrestrial environments, (b) exploitation of hosts which could be reached within the framework of these pyramids by the processes of host-range expansion and host-succession-extension.

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DISCUSSION

ANDERSON. — We have moved far from the idea that ascaridoids in elasmobranches are primitive. Would you care to comment ?

SPRENT. — I am unimpressed with the elasmobranchs as ancestral hosts because they appear to have only one endemic species in sharks and only three in rays. These do not appear to belong to a uniform group and may be aberrant rather than primitive. Moreover, their other ascaridoids such as *Terranova* are shared with other aquatic hosts.

BEVERIDGE. — Do you have any comment to make about the possible origin of *Baylisascaris tasmaniensis* in the Tasmanian devil (*Sarcophilus*) ?

SPRENT. — *Baylisascaris* is essentially a genus of northern carnivores, especially mustelids. It also occurs in South America. The most obvious possibility for its presence in a marsupial is that it was introduced with infected eutherians into Tasmania. Otherwise I have tentatively suggested a possible relation between the marsupial carnivores and the creodonts, but beyond this I have no explanation.

SCHAD. — With reference to the possibility that *Baylisascaris tasmaniensis* is a recent introduction into Tasmania — perhaps with ferrets imported from Europe. Why not infect some ferrets ? Perhaps it could be shown that *B. tasmaniensis* is merely a host determined variant of an holarctic *Baylisascaris*. Or perhaps it might prove to be a close relative of such a species — indicating rapid speciation in Australia.

SPRENT. — *B. devosi* is the only species actually grown in ferrets experimentally and its development could be compared with that of *B. tasmaniensis*. I am convinced that *B. devosi* and *B. tasmaniensis* are separate species and that the latter is more different from the Iormer than the former is from other species in the genus.

INGLIS. — I like your pyramid story which, if I have understood it fully, must mean that the evolution of the ascaridoids did not depend on the evolution of their final hosts. It must, I think, have depended on the infestation of a " new " host higher in the food triangle, either by the initial final host acting as an intermediate host or by a new intermediate host being picked up, either of which led to the isolation of the final host and its parasites. From this " new " parasite and host complex the ascaridoids would continue their spread and evolution. Have I understood your theory accurately and how much do we know about the host specificity of the intermediate hosts, when they exist ?

SPRENT. — I am suggesting (and again I stress it is speculation based on evidence which needs strengthening) that ascaridoids evolved independently of their hosts. I envision an evolution within the pyramids in two directions, one horizontal, the other vertical, each determined by feeding habits. In the horizontal directions in the second tier we have " host-range expansion " through sharing juvenile stages in the invertebrate prey. In the vertical direction we have " host-succession-extension " through adults in prey surviving in the predator after the prey has been eaten, egg laying being thus continued. The two host pattern now can become a three host pattern by subsequent suppression of the adult stage in the prey host. Host range expansion now can proceed at the top of the pyramid as it did in the second tier, so that multiple pyramids like a range of mountains are established with dominant predators on the peaks and an assortment of intermediate hosts within the massif.

Chabaud. — Je suis très heureux de voir que le Prof. Sprent tend à considérer les Crocodiles comme hôtes fondamentaux des Ascarides.

Les Crocodiles (et, parfois, les Tortues) apparaissent de plus en plus comme des hôtes privilégiés dans l'étude de groupes parasitaires variés. Ce sont par excellence des « hôtes anciens » car les représentants actuels diffèrent peu des formes de l'ère secondaire. Nous y retrouvons les ancêtres de beaucoup de groupes parasitaires (Coccidiomorphes, Filaires, Spirurides, Ascarides...).

Inglis. — I concur with Prof. Chabaud and like Prof. Sprent's story about crocodiles since there is no convincing evidence to show that freeliving marine nematodes have ever given rise to parasites. Nematodes have become parasitic from two groups of very different free-living nematodes, Rhabditida and Dorylaimida, both of which are almost wholly fresh-water or soil living. My picture would be of an origin in or near the edge of a body of freshwater, in a lake or estuary. In any case, the ascarids (certainly) and probably all nematode parasites developed relatively late in geological time.

Anderson. — I agree with Dr. Inglis. The implications seem clear : namely, that nematodes did not invade vertebrates until the evolution of the tetrapods. I personally believe ascaridoids had a terrestrial origin in vertebrates, developed heteroxenity and then transferred successfully to the aquatic milieu. I suggest the first intermediate hosts were vertebrates.

Sprent. — I feel that I am not qualified to comment on the aspects which concern the origin of the group because I am not sufficiently well versed on related groups. I did once suggest that ascaridoids might have been derived from free-living marine nematodes but evidently stuck my neck out too far. From the point of view of the diversity of hosts and their present distribution I would propose the estuaries of the great rivers of the old world tropics as the birth place of the ascaridoids.

Anderson. — I can understand the presence of ascaridoids in aquatic hosts if one starts with heteroxenous life-cycles — this is also the way certain lungworms were able to transfer to the marine environment with whales and seals. You have started, however, with an heteroxenous life cycle involving crocodiles and crustaceans, which is already rather advanced, what do you imagine was the situation prior to that ?

Sprent. — I agree that I have started with an heteroxenous cycle but that does not prejudice the possibility that there may have been a previous monoxenous cycle (I have always favoured the idea that there was one in a crustacean). As regards crocodiles, we do not know how they acquired their ascaridoids but in northern Australia, *C. porosus* acquires them when only 12 inches long and the 3rd stage larvae are extremely small (a few mm). Their diet appears to have been mainly crustacea and I think it may not be a " complex cycle " but just a simple two host pattern.

Czapliński. — What is your opinion about *Toxocara pearsei* which has been found in shrimps as an adult form. What is the general tendency of the life cycles of ascaridoids including (a) those in intermediate hosts (or hosts) in aquatic animals and (b) monoxenous forms in some terrestrial animals ?

Sprent. — *T. pearsei* was described by Chitwood but the specimens no longer exist. It would be very important if such a species existed because it would lend support to the concept that crustaceans were the original hosts of ascaridoids as I have suggested previously but without any support.

Prof. Anderson would I think agree to my envisioning an original monoxenity but this has become for almost all ascaridoids a two or three host pattern based on the life history pyramids. In three host aquatics pyramids, where known, there is often but not always a crustacean and a fish intermediate host. In terrestrial pyramids, there is usually a frog or a rodent and perhaps an invertebrate. But it is difficult to generalize, because so few life history patterns have been elucidated. In the relatively rare instances where non-carnivorous animals have become hosts for ascaridoids, special adaptations have evidently occurred, intermediate hosts have been lost and secondary monoxenous cycles have been established, transmission being effected through the placenta, milk, or through tracheal migration.